EVOLUTION OF THE GENUS *HOLMESINA* (PAMPATHERIIDAE, MAMMALIA)

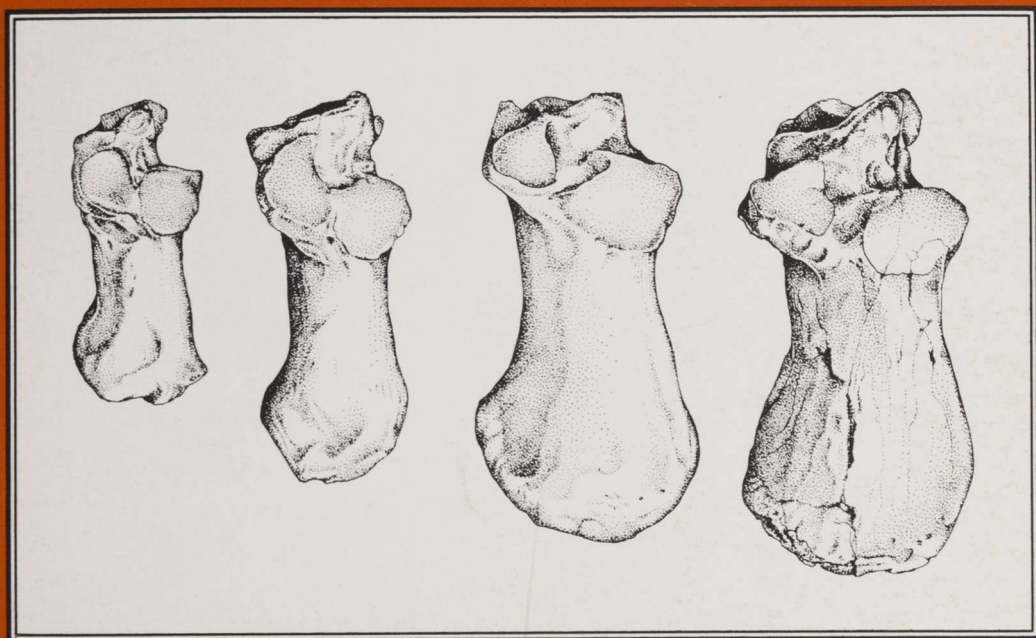### IN FLORIDA, WITH REMARKS ON TAXONOMY AND DISTRIBUTION.

A. Gordon Edmund

Pearce-Sellards Series

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GENUS *HOLMESINA*
(PAMPATHERIIDAE, MAMMALIA)

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TAXONOMY AND DISTRIBUTION.

A. Gordon Edmund

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ABSTRACT

A large series of specimens of pampatheres (fossil giant armadillos) has been found in Florida, covering approximately two million years from their emigration from South America to their late Pleistocene extinction. During this period, there was little morphological change, although the limb bones elongated by about 50%. The area of individual osteoderms, which is indicative of the surface area of the animal, increased, as expected, by the square of that amount, i.e. 2.2 times.

The generic name *Kraglievichia* Castellanos 1927, is incorrect for the Floridean Blancan species, as is *Pampatherium* Ameghino 1875 for the Rancholabrean species. *Holmesina* Simpson 1930 is the correct genus for the entire chronocline in Florida, with *H. floridanus* (Robertson 1976) for the Blancan species and *H. septentrionalis* (Leidy 1889) for the Rancholabrean and late Irvingtonian species. Specimens of Lujanian age from Ecuador, Peru, and Venezuela are provisionally referred to *Holmesina occidentalis* (Hoffstetter 1948), and those of the same age from Brasil are provisionally referred to *Holmesina humboldti* (Lund 1839). No ancestral forms are currently recognized among either the published or unpublished material from South America.

RESUMEN

Un buen numero de especĭmens de pampaterios (armadillos gigantes fósiles) han sido encontrados en Florida, abarcando un lapso de aproximadamente dos millones de años, desde su inmigración de Sud América hasta su extincíon en el Pleistoceno tardío. Durante este periódico pocos cambios morfológicos se presentaron, ha pesar de que los huesos apendiuclares se alagaron en un 50%. El area de las placas óseas individuales, la cual es indicativa del area superficial del animal, aumentó, como era esperado, al cuadrado de esa cifra i.e. 2.2 veces.

El nombre genérico de *Kraglievichia* Castellanos 1927, originalmente asignado a la especie Blanqueana de Florida es equivocado, como lo es también *Pampatherium* Ameghino 1875 para la especie Rancholabreana.

Yo propongo que el género *Holmesina* Simpson 1930, sea reconocido como válido para la cronoclina completa de Florida; con *H. floridanus* (Robertson 1976) para la especie Blanqueana y *H. septentrionalis* (Leidy 1889) para la Rancholabreana.

Las especies del Pleistoceno tardío, *H. occidentale* (Hoffstetter 1948) del Ecuador, Perú y Venezuela, y *H. humboldti* (Lund 1839) del Brasil posiblemente puedan ser referidas también como *Holmesina*.

Se han buscado posibles ancestros entre el material sudamericano publicado y no publicado, pero ninguno parece ser eligible.

ACKNOWLEDGEMENTS

ABBREVIATIONS AND ACRONYMS

AMNH   American Museum of Natural History, New York
FSM   Florida State Museum, University of Florida, Gainesville, Fla.
IRV   Irvingtonian Land Mammal Age
O.R.   Observed Range
RHB   Private Collection, Roy and Helen Burgess, Venice, Florida
RLB   Rancholabrean Land Mammal Age
ROM   Department of Vertebrate Palaeontology, Royal Ontario Museum, Toronto
ROM:B Brayfield Collection, Royal Ontario Museum

For data on collecting sites, refer to Webb 1974 or Kurtén and Anderson 1980.

KEY WORDS

Pampathere, Armadillo, *Holmesina, Chlamytherium, Pampatherium, Kraglievichia,* Edentate, Xenarthra, Evolution.

INTRODUCTION

Robertson (1976) described a small pampathere of late Blancan age from the Haile XV A site in Florida. He recognized that it was the oldest pampathere yet described in North America, and called attention to the fact that there is an adequate series of specimens covering the time period between the Blancan and late Rancholabrean. Although the Haile XV A material includes pieces of skull and mandible, as well as post-cranial elements, the diagnostic anterior teeth or alveoli are lacking except for two isolated lower teeth. Robertson also described additional elements from two Blancan sites on the Santa Fe River to supplement his description.

On the basis of size, general morphology and geological age, Robertson referred his pampathere to the Argentinian genus *Kraglievichia* Castellanos 1927, with the new species name *floridanus*. He also reviewed the taxonomy of the pampatheres and concluded that *Pampatherium* Ameghino 1875 was the correct name for the late Pleistocene form in North America rather than *Holmesina* Simpson 1930.

This paper examines the mass of pampathere material from North America, mainly from Florida, to document more thoroughly the chronocline from the Blancan to the Rancholabrean form. It also provides evidence that the generic names *Kraglievichia* and *Pampatherium* are not applicable to North American species and traces the history of discovery and taxonomy of pertinent North American forms. All specimens known from North and Central America belong to the *Holmesina* lineage with the exception of material from three Pleistocene sites in Mexico.

MATERIAL

The first adequate pampathere material of Blancan age from North America is that from the Haile XV A site, Alachua Co., Florida, well described by Robertson (1976). The holotype, FSM 10902 is a very fragmentary skull. Most of the other Haile XV A pampathere bones were originally numbered FSM 10902, the same as the type skull, but bacause elements of more than one individual (probably three) are present, these have been given separate numbers, with FSM 10902 retained for the skull. Judging from the state of preservation and various matching articulations, I agree with Robertson (op. cit. p. 124) that many of the bones probably belong to a single individual. Robertson listed the bones from other Blancan sites as Referred Material, and more has been collected and identified in the interim. I have also examined and measured all available *Holmesina* material of Irvingtonian and Rancholabrean ages. The most extensive Irvingtonian collection (Inglis IA, Citrus Co.) is from early in the Irvingtonian. Much of the size increase in *Holmesina* apparently occurred during the Irvingtonian. Late Irvingtonian

sites such as Kanopolis, Kansas, (Hibbard et al. 1978), or McLeod, Florida (Kurtén & Anderson 1980) produce specimens within the expected size range of *H. septentrionalis*.

The largest samples, as would be expected, are Rancholabrean. Among these are FSM 9336, a very well preserved individual lacking the skull, from Branford, Suwanee Co.; RHB 3151, from Sarasota Co., less well preserved and also headless, but with much of the skeleton and carapace; and numerous suites of specimens from other localities in Florida. One of the best described specimens is that of James (1957) from Houston, Texas, and there are many excellent elements at Austin, Texas, including those from Ingleside, San Patricio Co., described by Lundelius (1972). Specimens from outside Florida, apparently all Rancholabrean, will be described and compared in a subsequent paper. Certain specimens from Texas are particularly interesting because of their resemblance to *H. humboldti* from Brasil.

HISTORY OF NORTH AMERICAN COLLECTING

The first North American pampathere specimens were osteoderms collected near Arcadia on Peace Creek (now Peace River, De Soto Co.) in Florida in 1888. Leidy (1889a) first described them as *Glyptodon septentrionalis* but later (1889b) referred them to the Brasilian species *Chlamydotherium humboldti* Lund 1839. Sellards (1915a, 1915b) described further material from other parts of Florida, including most of a right mandible and many osteoderms. He recognized these as being different from *C. humboldti* and revived Leidy's specific name in the combination *Chlamytherium septentrionalis* (see taxonomic section below). In 1922 Cahn reported an excellent mandible from Brazos Co., Texas, which he identified as *Chlamytherium septentrionalis*. The original specimen was deposited in the museum of the Texas Agricultural and Mechanical College, but could not be located. Good casts exist in AMNH (No. 13221) and ROM (No. 6466). The presently valid generic name *Holmesina* was erected by Simpson (1930), the description being based on the premaxilla, maxilla, mandible, and associated osteoderms of a single individual (AMNH 26856) from Manatee Co., Florida, which Simpson designated the neotype.

In subsequent years numerous remains of pampatheres continued to be collected. A large proportion of these are in the Florida State Museum, but there is also fine material at Austin, Texas; Ann Arbor, Michigan; Toronto, Canada; Los Angeles and Berkeley, California; and in several private collections in Florida. Included in these are numerous specimens dating from late Blancan and Irvingtonian as well as the much more prolific Rancholabrean. This material is now adequate to permit a review of the North American species, and to document their history since their first appearance in the Blancan.

TAXONOMIC HISTORY PERTINENT TO NORTH AMERICA

The nomenclature of the fossil giant armadillos has had a long, confused history. In 1839 the name *Chlamytherium humboldti* Lund was published for material from Pleistocene cave deposits in the State of Minas-Gerais, Brasil. Lund had intended the generic name to be *Chlamydotherium* (Paula Couto 1954, 1956). Lund's manuscript, dated November 16, 1837 contained the correct spelling, *Chlamydotherium* and thus the published version was a typographical error. Lund subsequently used the correct spelling, as did many later authors (see Paula Couto 1956, pp. 13-14). To complicate matters further, it was discovered that Bronn (1838) had proposed *Chlamydotherium* for a glyptodont, making the name unavailable for the fossil giant armadillo. Ameghino (1875) realized this situation and erected the genus *Pampatherium* to include a new species from Argentina *(P. typum)* as well as Lund's species *humboldti*. Ameghino later dropped the generic name *Pampatherium* except when used for *P. typum*. In 1883 he briefly described the early Pliocene species *C. paranense* in the genus *Chlamydotherium*, and subsequently (1888) *C. intermedium* in the same genus. Moreno and Mercerat (1891) described the oldest pampathere then known (Hayquerian, late Miocene) as *Chlamydotherium minutum*. Further material was assigned to the same species by Rovereto (1914). The same author (op. cit. p. 223) also erected a new species, *Chlamydotherium subintermedium* on the basis of three isolated osteoderms.

The most recent catalog of dasypodids of Argentina, (Scillato Yane 1980) followed Paula Couto (1954) by retaining *Pampatherium*, with *P. typum* as the genotype of the Pampatheriinae. It did not recognize *Chlamytherium* or *Chlamydotherium*. I agree with the rejection of these two names, and any derivatives thereof. The valid type genus is *Pampatherium* Ameghino 1875.

Moreno and Mercerat (1891) recognized the family Chlamydotheriidae, and Rovereto (1914) placed his *C. minutum* in the Chlamydotheriidae. Lydekker (1894) recognized the Chlamydotheriinae as a subfamily of the Dasypodidae, ignoring Ameghino's (1875) proposal to use *Pampatherium* as the type genus for both the Brasilian and Argentinian late Pleistocene species and his recognition in 1889 of the family Chlamydotheriidae.

The group was given superfamilial status when Bordas (1939a) recognized its conservatism and longevity, and erected the superfamily Chlamydotherioidea. Hoffstetter (1969) however, followed Patterson (1967) in maintaining the Pampatheriinae as a subfamily.

Thus, there are historically two schools of thought regarding the correct familial or subfamilial name of the group. The weight of evidence would appear to leave no question of the validity of *Pampatherium* as the type genus of the subfamily Pampatheriinae. With the exception of Castellanos,

no student familiar with both the North and South American material continued to use *Chlamytherium* or *Chlamydotherium*, nor the common name chlamythere. References for this position include Romer (1966), Hoffstetter (1969), Patterson and Pascual (1972), Marshall, Hoffstetter and Pascual (1983) and Cartelle and Bohorquez (1985).

Unfortunately, this acceptance has not been universal. James (1957) described a pampathere from Texas, and recognized *Chlamytherium* as valid in the late Pleistocene of North America. He further suggested that the family Chlamytheriidae (=Chlamydotheriidae Ameghino 1894) might be well founded. Lundelius (1972) followed James in using *Chlamytherium septentrionalis*, but assigned it to the family *Dasypodidae*. Robertson (1976) agreed with James in rejecting *Holmesina* and accepted *Pampatherium* as the valid genus to include the species *septentrionalis*. He also placed *Pampatherium* in the family Dasypodidae without designation of a subfamily, but refers to various species of fossil giant armadillos as chlamytheres.

In my description of pampathere armor (Edmund 1985a), I considered the giant armadillos to be a distinct family, the Pampatheriidae. Paula Couto, in an uncompleted manuscript given to me in 1981, recognized the family Pampatheriidae (Paula Couto 1958) but the manuscript lacks a bibliography. In his Paliomastozoologia (1979) he describes the subfamily Pampatheriinae Paula Couto 1958, but without a citation. The 1981 assignment to familial rank may be a *lapsus*, but he clearly lists it under the Superfamily Dasypodoidea Simpson 1931. I agree with Paula Couto's 1981 opinion, and recognize the fossil giant armadillos as a separate family. From their earliest appearances, Friasian of Colombia and Chasicoan of Argentina, pampatheres have been quite distinct from glyptodonts and dasypodids, and have maintained a conservative suite of distinguishing characters as follows:

    —Armadillos of large size (up to 3 m in length) with a robust skeleton. Manus and pes digitigrade, without extreme fossorial adaptations.
    —Carapace divided by three transverse bands of imbricating osteoderms. All carapacial osteoderms relatively large, each bearing in life a single keratinous scute.
    —Caudal armor typically one ring of osteoderms per vertebral segment.
    —Mandible robust, deep dorsoventrally, with the coronoid process and condyle raised well above the occlusal level. Articular surfaces of condyle and glenoid essentially flat.
    —Dental formula 9/9, with the most anterior teeth cylindrical and at least the posterior five bilobate in section. Occlusal surfaces flat, often with transverse striae, indicating herbivorous diet. All teeth permanently open-rooted.
    —Premaxilla bears one tooth, but with the suture for the maxilla passing through the second alveolus.

—Skull pneumatic, with a series of large sinuses in the maxilla, frontal and alisphenoid.
—Jugal well developed, with a suborbital flange for the masseter muscle. Similarly the prominent pterygoid processes provide strong attachments for the pterygoid muscles.
—Cervical vertebrae II to V coossified, as well as Cervical VII and Thoracics I and II.
—Pelvis massive, the posterior part formed by greatly elongated and flattened transverse processes of at least three, and perhaps as many as five or six caudal vertebrae fused to the ischium. A broad, laterally compressed process descends to meet the pubis, enclosing the large sacroischiac fenestra, larger than the obturator foramen. The synsacrum consists of approximately nine vertebrae.

Some of these characters are found also in the Dasypodidae *s.s.* and Glyptodontidae, but the pampatheres have an adequate suite of distinctive characters to merit recognition as a family.

Alfredo Castellanos, the foremost student of Argentinian pampatheres, (1927, 1937, 1946, 1958) followed Ameghino's abandonment of the genus *Pampatherium* and the derived subfamilial name. He retained the species *typum* and *humboldti* but placed them first (1927) in the genus *Chlamydotherium* and subfamily Chlamydotheriinae. In his subsequent publications he used *Chlamytherium*, Chlamytheriinae and the common name clamiterios.

SUMMARY OF PAMPATHERE SYSTEMATICS

The main thesis of this paper is the documentation of a chronocline leading from the Blancan *H. floridanus* to the Rancholabrean *H. septentrionalis.* However, because of the confusing plethora of inappropriate generic names in the recent North American literature (James 1957, Lundelius 1972, Robertson 1978) a summary of pampathere systematics, as I currently perceive it, is pertinent.

Scillato Yane (1980) conveniently listed all genera and species recognized from Argentina, along with an exhaustive synonymy. Literature on taxa from other South American countries is scattered, and the entire group requires thorough revision. Castellanos (1927, 1937, 1946) proposed a lineage of pampatheres increasing in size and in degree of anterior "molarization", covering the time period from the Chasicoan (Upper Miocene) to the Lujanian (Upper Pleistocene). Three generic names, *Vassallia, Plaina,* and *Pampatherium* were assigned to parts of this apparently continuous lineage. *Kraglievichia paranense* was erected by Castellanos (1927, 1937) for a small pampathere typified by peculiarly ornamented osteoderms, and apparently ranging from the Chasicoan to the Montehermosan (Upper Miocene to

Lower Pliocene). It may be closely related to *Vassallia* but the material re-
covered to date is inadequate for a decision.

Another taxon, as yet unnamed, is known from the Montehermosan of
Argentina, and is represented only by numerous isolated small osteoderms
with clearly demarcated submarginal bands and narrow central keels. Very
similar, if not identical osteoderms were collected on the Rio Juruá in the
state of Acre in Brasil in 1956 by G.G. Simpson and Carlos de Paula Couto
(unpublished).

Similar but not identical osteoderms are associated with cranial and ske-
letal elements from the Friasian La Venta locality of Colombia (Marshall,
Hoffstetter and Pascual 1983). Isolated osteoderms from this site were
referred to *Kraglievichia* by Porta (1962), but this was an error in identifi-
cation. The La Venta material represents the oldest known typical pampa-
there, since the status of the Eocene genus *Machlydotherium* is still unclear.

The Brasilian species *Holmesina humboldti* (Lund 1839), along with
several synonymic species names, have been referred to various genera, most
often to *Pampatherium* (Cartelle and Bohorquez 1985). I believe it is more
closely related to *Holmesina* and refer it to that genus pending more detailed
study.

Also probably referable to *Holmesina* is the species *H. occidentale*
Hoffstetter 1952, referred to *Chlamytherium* by Hoffstetter (1952), to *Hol-
mesina* by Hoffstetter (1953) and to *Hoffstetteria* by Castellanos (1957). I
have collected a large series of this species from Peru and Ecuador and have
also recognized identical specimens from western Venezuela. Cartelle and
Bohorquez (1985) described *Pampatherium paulacoutoi* from Bahia, Brasil.
Their measurements and descriptions agree closely with the *occidentale*
material at the Royal Ontario Museum and may prove synonymous. I agree
with Hoffstetter that *Holmesina* is probably the most appropriate genus for
occidentale, and that it is not closely related to the *Pampatherium* lineage.
Unfortunately, Pliocene and early Pleistocene sites are essentially unknown
in Central America and the northern part of South America, making it
difficult to do more than speculate on the history and relationship of *Hol-
mesina* in Florida and in South America (Robertson 1976, p. 142).

INCREASING SIZE OF HOLMESINA IN FLORIDA

Robertson (1976) described pampathere material from the late Blancan site Haile XV A, and compared various elements to those from Irvingtonian and Rancholabrean sites in Florida. He clearly demonstrated a large increase in size during this period of approximately two million years (Savage and Russel 1983). In addition to the elements figured by Robertson, osteoderms and other bones have been measured wherever adequate material exists for comparison. Unfortunately, elements comparable at intervals during the Blancan, Irvingtonian and Rancholabrean are few, so that statistical treatment is not possible. The Irvingtonian, in particular, is represented mainly by one very rich but early site (Inglis I A) and by a single very late individual (the McLeod site). Thus, in many cases the comparison can be made between only Blancan and Rancholabrean. In this section, all material is from Florida.

CARAPACE

The morphology of typical buckler and imbricating osteoderms is given in Edmund 1985a. In both types of osteoderms a depressed marginal band extends completely around the buckler osteoderms, and around much of the ornamented area of the imbricating osteoderms. It is generally one to three millimeters wide, and is rugose and pitted (Fig. 1A). Concentric within this marginal band is the submarginal band, usually prominently raised above the marginal band and the depressed central area. It varies in height and width, but is generally narrow (2 - 4 mm) and clearly elevated. The raised central figure is variable, but is separated from the submarginal band by a depressed, usually finely punctate area termed the sulcus.

In *Holmesina septentrionalis*, especially in large, well-preserved individuals, the features described above are usually strongly expressed. In the early Irvingtonian and Blancan specimens, the relief of the surface features is less pronounced, but still clear (Fig. 1B). This ornamentation separates the *Holmesina* group from the feebly ornamented *Vassallia - Plaina - Pampatherium* group . In the latter, the marginal depressed band is usually absent or variable, and the depressed area between the submarginal band and central figure is absent or very feebly expressed (Edmund 1985b). *Kraglievichia* has an ornamentation that apparently is unique (Fig. 1C), although definitely associated skeletal and carapacial material is unknown. The remainder of this section will deal with *Holmesina* osteoderms from Florida only, so as to limit the variability attributable to geographic variation.

It is assumed that the number of osteoderms in each carapace is nearly constant, and that an adequate sample of osteoderms reflects the size of the individual. I make this assumption mainly on the basis that small (Blancan) specimens have small osteoderms, but that the shapes and proportions are

Table 1. Increase in osteoderm size between Blancan and Rancholabrean samples.

Type	Land Mammal Age	O.R. Area	N	$\overline{X}$
Buckler	Blancan	678–751	40	714
''	RLB	1368–1970	88	1628
Imbricating	Blancan	1675–1802	20	1738
''	RLB	3399–4148	23	3847

Increment ratio (Buckler) 1628/714 = 2.28
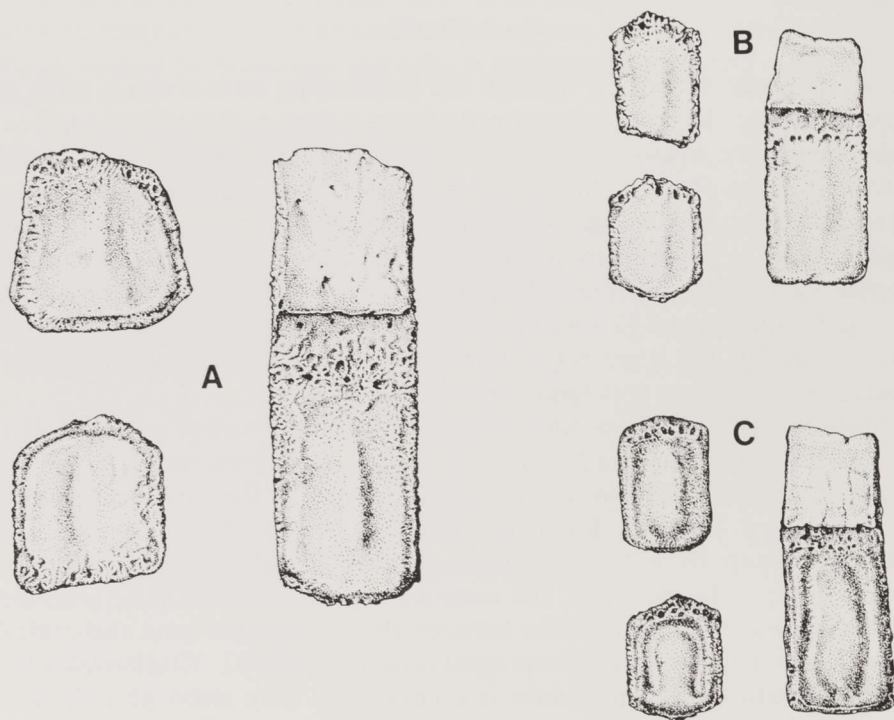Increment ratio (Imbricating) 3847/1738 = 2.21

Fig. 1. Two buckler and one imbricating osteoderms of each of three species of pampatheres. A) ROM:B 7960 *Holmesina floridanus*, Blancan, El Jobean, Charlotte Co., Florida. B) FSM 9336 *Holmesina septentrionalis*, Rancholabrean, Branford, Suwanee Co., Florida. C) ROM 23829 *Kraglievichia paranense*, Montehermosan, Entre Ríos, Argentina.

similar to those of larger, Rancholabrean individuals. Further, the genus is exceptionally conservative. Unfortunately nothing has been reported in the literature regarding variability in number of osteoderms, either in modern armadillos or in the fossil record. Table 1 displays the "area" —i.e. length times width, for both imbricating and buckler osteoderms, plotted against time as represented by land mammal ages. Each sample represents the mean of at least ten osteoderms from a single individual or a single site. Between the Blancan and Rancholabrean, the area of both the buckler and imbricating osteoderms increased by a factor of 2.2, suggesting that the body surface area increased approximately 2.2 times. This should correlate with the increasing size of the skeleton, using the formula $\Delta L^2 \propto \Delta A$, where L is the length of the skeletal element and A is the surface area. The mean for the squares of limb bone length (Table 2) increase is 2:26, virtually equal to the increase in osteoderm area. This is one of the few instances in which this relationship can be confirmed for vertebrate fossil material.

LIMB BONES

Robertson (1976) compared the femora and calcanea of Florida *Holmesina* of various land mammal ages by photographs in his figures 8 and 9, but did not compare measurements. Comparable elements are not always available for all three land mammal ages, but some can be obtained over the entire period (Table 2). During the time from Blancan to Rancholabrean, the lengths of the radius, tibia-fibula and calcaneum increased by approximately one and a half times (Table 2). As noted by Robertson (op. cit.), there is no obvious change in morphology of the tibia-fibula or the radius. Although one might expect the Rancholabrean animals to have stouter long bones than the Blancan animals, this is not always the case. The ratios of distal width to total length of the tibia-fibula are shown in Table 3. The Rancholabrean sample appears to be ten percent more robust than the Blancan, but the sample size, especially in the Blancan, is small.

Table 2. Increase in bone lengths from Blancan to Rancholabrean times.

Element	Blancan Mean Length	Rancholabrean Mean Length	Ratio of RLB length to Blancan length	Ratio squared
Radius	90	133	1.48	2.18
Tibia-fibula	136	195	1.43	2.06
Calcaneum	64	102	1.58	2.54
		Means	1.50	2.26

Table 3. Changes in tibia-fibula measurements from Blancan to Rancholabrean times.

Land Mammal Age	N	Distal Width		Length		Ratio of Distal W. to Length
		O.R.	$\overline{X}$	O.R.	$\overline{X}$	
RLB	6	78–93	84	185–213	195	0.43
Blancan	6	47–60	54	122–151	136	0.39

Table 4. Changes in radius dimensions from Blancan to Rancholabrean times.

Land Mammal Age	N	Distal Width		Length		Ratio of Distal W. to Length
		O.R.	$\overline{X}$	O.R.	$\overline{X}$	
RLB	2	41–41	41	131–135	133	0.31
IRV	2*	36–36	36	133–133*	133	0.25
Blancan	3	19–22	21	88–94	90	0.23

*left and right of same individual (Yarmouthian)

Table 5. Changes in calcaneum dimensions from Blancan to Rancholabrean times.

Land Mammal Age	N	Tuber Width		Length		Ratio of Tuber W. to Length
		O.R.	$\overline{X}$	O.R.	$\overline{X}$	
RLB	4	46–52	49	95–107	102	0.48
IRV	4	35–40	37	80–102	89	0.42
Blancan	4	26–26	26	63–64	64	0.41

Because of inadequate samples, the only other long bone available on which to check this trend is the radius (Table 4). Distal width was divided by total bone length, indicating an increase in robustness over the three land mammal ages. The percentage increase from Blancan to Rancholabrean is 30 percent. This is based on a total of only seven specimens.

A larger sample is available for the calcaneum (Table 5), showing that it increases both in total length and width of tuber calcanei. The tuber be-

Table 6. Changes in the ratio of tuber to neck in the calcaneum from Blancan to Rancholabrean times.

Land Mammal Age	N	Tuber Width		Neck Thickness		Ratio of Tuber W to Neck Thickness
		O.R.	$\overline{X}$	O.R.	$\overline{X}$	
RLB	5	46–52	49	16–19	17	2.7
IRV	4	35–40	37	14–17	15	2.5
Blancan	2	26	26	11–12	11.5	2.3

Table 7. Changes in the separation of medial and lateral facets on the calcaneum and astragalus from Blancan to Rancholabrean times.

Land Mammal Age	Calcaneum			Astragalus		
	N	O.R.	$\overline{X}$	N	O.R.	$\overline{X}$
RLB	4	3–7	6	5	4–7	6
IRV	3	0–1	0.3	4	2–5	3
Blancan	2	0	0	0	-	-

Table 8. Changes in dimensions of facets on the calcaneum from Blancan to Rancholabrean times.

Land Mammal Age	N	Medial facet "Area" = LxW		Lateral facet "Area" = LxW		Areal Ratio of Medial facet to Lateral facet
		O.R.	$\overline{X}$	O.R.	$\overline{X}$	
RLB	4	210–397	303	384–696	516	0.59
IRV	4	195–266	238	320–468	401	0.59
Blancan	4	117	117	204	204	0.57

comes more prominent and rounded, and increases in width faster than length (Fig. 2 and Table 5). Another change, noted by Robertson, is that the tuber becomes expanded relative to the post-articular segment. This is shown in Table 6, in which the tuber width is divided by minimum thickness of the neck. The increase is quite regular during the three stages, giving a total increase of 16 percent.

The other major change, as noted by Robertson, is in the separation of the two facets for articulation between the astragalus and calcaneum (Fig. 2 and Table 7). In the two available calcanea from the Blancan, the two facets are thoroughly confluent over a length of several millimeters, the distinction indicated only by a change of angle. By early Irvingtonian time (Inglis I A) the facets are discrete, but still in contact in two of the three known specimens, and in the Rancholabrean they are always separate. No astragalus is known from the Blancan, but those from the Irvingtonian and Rancholabrean show considerably wider separation of facets than in the corresponding calcanea.

Robertson also mentioned that the two facets are nearly equal in size in the Blancan form, but that the lateral facet is much larger in the Rancholabrean. In the case of the Rancholabrean specimen FSM 9336, which Robertson had for comparison, the medial facet is particularly small. To resolve this problem with a larger sample, the length and width measurements of the facets of a number of specimens were compared (Table 8). The difference appears minimal, although the number of specimens studied is small.

It should be noted that the analyses of the calcaneum are based on fairly small sample sizes. However, there is no evidence to the contrary, and I feel confident that larger sample sizes would only give added weight to the conclusion of gradualism. The same observation applies to the study of the metapodials.
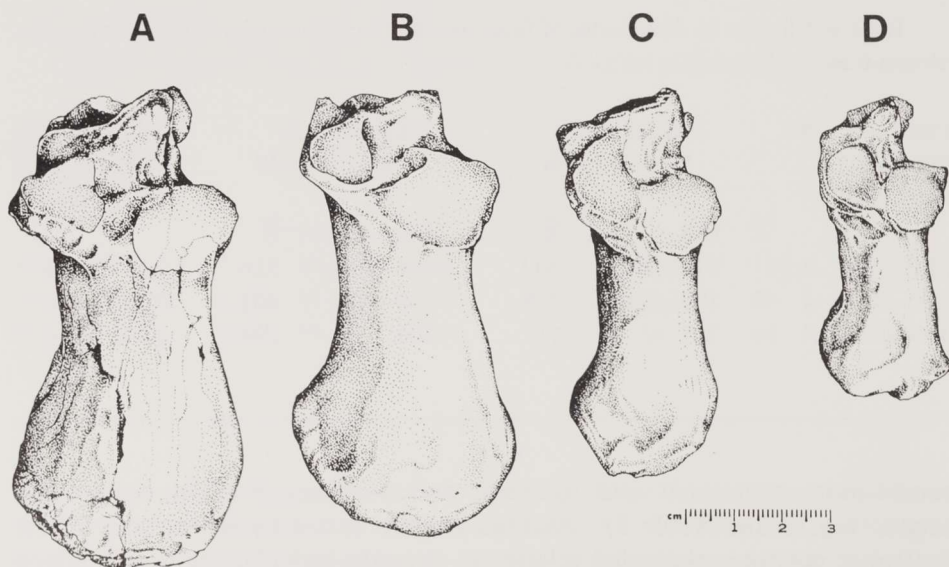

Fig. 2. Left calcanea of Floridean species of *Holmesina*. A) RHB 3151 *H. septentrionalis*, Rancholabrean, Sarasota Co. B) FSM 20954 *Holmesina* sp., Irvingtonian, Haile XVI A (reversed from right). C) FSM 20946 *Holmesina* sp., Irvingtonian, Inglis I A. D) ROM 21803 *H. floridanus*, Blancan, Haile XV A (cast).

METAPODIALS

Metapodials, especially numbers II to IV, are among the most frequently pre-
served skeletal elements of pampatheres. All specimens with adequate data
are plotted in Figs. 3 and 4, which show a clear increase in size from Blancan
to Rancholabrean. The mean increase in length for metatarsals II, III and
IV, and metacarpals II and III is 1.6 times. Metacarpal IV, however, shows
an ultimate increase of 10 percent. It had increased from 28 mm for a
single Blancan example to a mean of 39 mm in the Irvingtonian (N = 3), then
diminished to a mean of 30 mm in the Rancholabrean (N = 3). This reversal
may well reflect a real trend, considering that the range of measurements
does not overlap and that the means are well separated. A larger sample, es-
pecially with late Irvingtonian specimens, might cause the length ranges in
the Irvingtonian and Rancholabrean to become confluent, but I would not
expect the downturn of size to be affected.

The morphology of the metapodials is fairly constant during the relevant
time period, except for the features noted by Robertson. The metapodials
of Irvingtonian specimens resemble those of the Rancholabrean more closely
than they do those of the Blancan.

TAXONOMIC CONCLUSIONS

Robertson (1976) erected the name *Kraglievichia floridanus* for the Blancan
species of pampathere from Florida, based partly on Castellanos' (1927,
1937) descriptions of *K. paranense* from the lower Pliocene of Argentina,
and partly on osteoderms from the La Venta Miocene of Colombia identified
incorrectly as *Kraglievichia* by Porta (1962). Robertson had access to a
larger suite of material from Colombia, and suggested that it might better be
referred to Castellanos' (1927) genus *Vassallia*.

He drew attention to the fact that in the Florida Blancan specimens the
two calcaneal facets on the astragalus (i.e. ectal and sustentacular) are con-
fluent, separated only by a change in angle (Fig. 2). I have recently com-
pared the Florida specimen with newly prepared astragali and calcanea from
La Venta, and the structure of the astragalo-calcaneal articulation is quite
different. In the La Venta animal the two facets are not only separated by a
gap of some three millimeters (in both astragalus and calcaneum) but also by
a difference in elevation of the facets. This presumably derived feature rules
out the La Venta pampathere from ancestry of *H. floridanus* since it would
require the facets to become confluent then to separate during the Plio-
Pleistocene, an unlikely event.

The ornamentation pattern of the La Venta osteoderms is generally simi-
lar to that of the North American *Holmesina* lineage, however, suggesting at
least some degree of relationship. The La Venta animal is also distinct from
the *Vassallia - Plaina - Pampatherium* lineage, based on osteoderm ornament-

ation and absence of rectangular osteoderms in the pelvic buckler (Edmund 1985A).

Kraglievichia paranense can be distinguished from the La Venta animal, the *Holmesina* lineage, and the *Pampatherium* lineage by its characteristic osteoderms (Fig. 1C). Although many specimens, including a fine skull, are known from Argentina, in no example are the cranial, post-cranial and carapacial elements associated. It is unfortunate that the type skull of *H. floridanus* is so incomplete, precluding more detailed comparison with small species from South America.

The animal described by Robertson (1976) is essentially a small version of *Holmesina septentrionalis*. The osteoderms are quite dissimilar to those of *Kraglievichia* and of the *Pampatherium* lineage, and the calcaneo-astragalar articulation rules out descent from the La Venta animal. Its ancestry
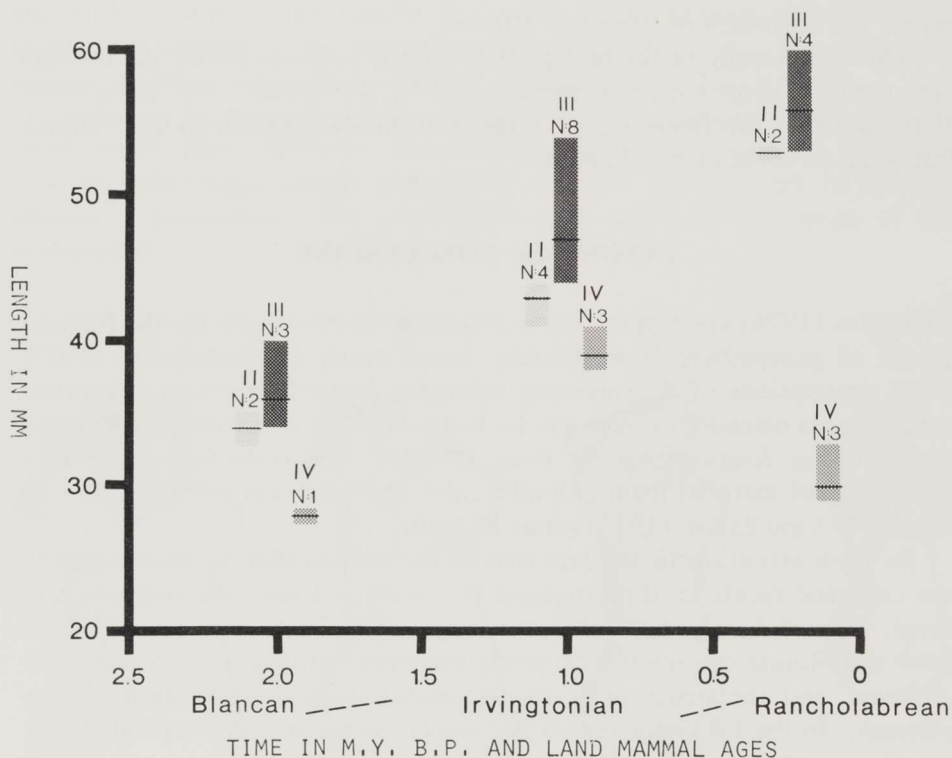

Fig. 3. Relation between metacarpal length and time in *Holmesina* from Florida.

may lie with an as yet undescribed taxon with small, keeled osteoderms from the Montehermosan of Argentina. For the purposes of this paper, it is sufficient to conclude that *Holmesina* of North America does not have close relationships with any described pre-Pleistocene South American taxon or lineage. Cranial and dental morphology are of little use for this purpose since there is almost no comparable pre-Pleistocene South American material except that assigned to *Kraglievichia, Vassallia* or *Plaina*. Thus, *Holmesina* is the valid genus for the Florida material, with *H. floridanus* Robertson 1976 in the Blancan and *H. septentrionalis* (Leidy 1889) Simpson 1930 in the Rancholabrean and probably also the late Irvingtonian. Specimens from early and middle Irvingtonian, intermediate in size, are referred only to *Holmesina* sp., because a new specific name is unwarranted.
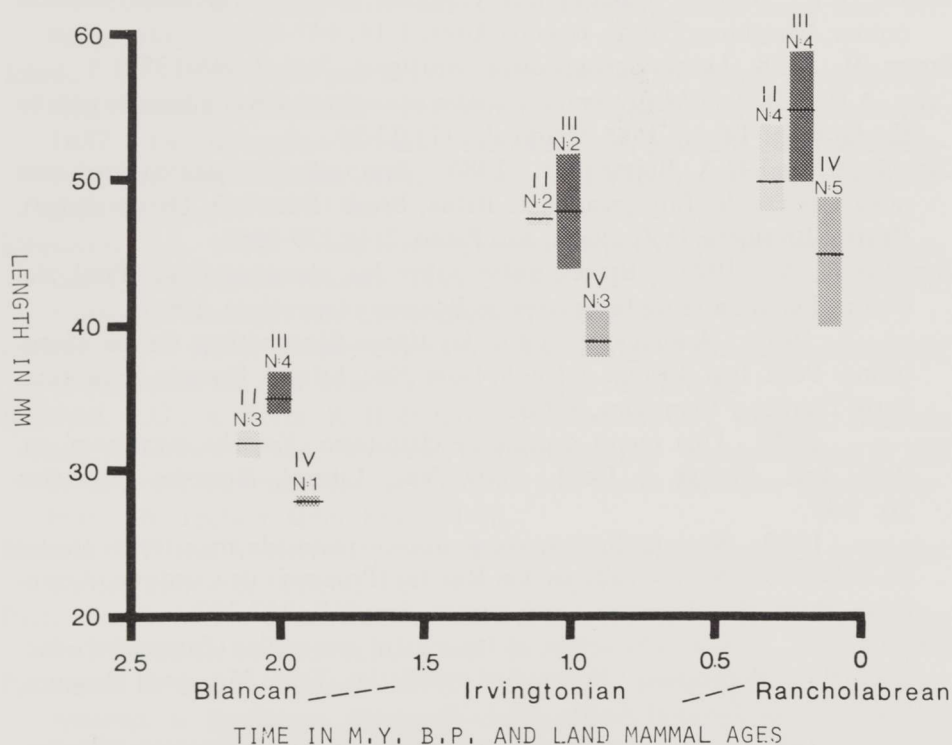

Fig. 4. Relation between metatarsal length and time in *Holmesina* from Florida.

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